

## Development of the Orangutan Permanent Dentition: Assessing Patterns and Variation in Tooth Development

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**ABSTRACT** This study examines dental formation and alveolar emergence in a large cross-sectional sample composed primarily of wild-reared orangutans ( $N = 89$ ) in order to provide information on the development of the permanent dentition in this hominoid and to address questions of variation in individual tooth formation, between teeth and between individuals. All specimens have been radiographed in lateral aspect and stages of crown and root formation recorded for all teeth. The ranges of crown and root formation of  $I_1$ ,  $C_1$ ,  $P_4$ ,  $M_2^2$ , and  $M_3^3$  have been calculated relative to the stage of  $M_1^1$  development within a specific tooth quadrant. Then, for each specimen, BMDP scatterplot and nonparametric statistics have been used to graph changes in stages of these teeth relative to  $M_1^1$  stages and to examine relationships between pairs of upper and lower dental counterparts and between teeth of each jaw. Results indicate 1) high correlations between upper and lower tooth pairs and between many of the permanent teeth within individuals, 2) a relatively large range of variability in individual tooth development (multi-stage ranges relative to  $M_1^1$ ), 3) greater variation in root development at emergence than earlier reports, and 4) evidence of variability within the sequence emergence pattern of the orangutan. © 1996 Wiley-Liss, Inc.

Numerous studies have advocated the use of formative phases of the dentition in establishing physiological age because of the relative lack of influence on developing teeth by environmental or other factors (e.g. disease, nutrition, etc.) (Garn et al., 1965a,b; Lewis and Garn, 1960). As such, tooth emergence and state of calcification are commonly used to establish age at death of specimens derived from various sources, i.e., forensic, archaeological, and paleontological. These developmental indicators have also been used to estimate age at death of hominid fossils by comparison with the developing dentitions of extant hominoids. However, comparisons between fossil hominids and living hominoids have resulted in differing interpretations of the rate (and indirectly age), pattern,

and range of variability of hominoid dental development (Beynon and Dean, 1987, 1988, 1989; Bromage and Dean, 1985; Bromage, 1987; Dean, 1987a,b, 1989; Dean et al., 1993a; Mann, 1975; Mann et al., 1987, 1989; Simpson et al., 1991; Smith, 1986, 1987, 1989a,b, 1991, 1994; Wolpoff et al., 1988).

Much of the difficulty in analyzing hominoid dental development is due to difficulties in establishing differences between ape and human dental development. Several studies suggested that apes and humans differ in several developmental relationships (Anem-

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one et al., 1991; Dean and Wood, 1981; Schultz, 1940, 1941). First, the first molars emerge into occlusion chronologically earlier in the great apes followed, after a hiatus, by emergence of the central incisors; typically, these teeth emerge through the gingiva coincidentally in humans. Thus, the human central incisor is more fully formed at the time of M1 gingival emergence than is the central incisor of great apes. Second, in great apes, the canine emerges late in the eruption (gingival emergence) sequence. Therefore, this tooth goes through a relatively longer period of development than in humans. Third, great apes are distinguished from humans by having greater developmental overlap between sequential molars; i.e., calcification of the second and third molar crowns commences prior to, or coincident with, completion of crown formation of the molar immediately anterior to them in the tooth quadrant (the first and second molar respectively).

Simpson et al. (1991), Smith (1986, 1991, 1993), Mann et al. (1987), and Conroy and Vannier (1991a,b) investigated potential relationships between the patterns discussed above and developmental rate in the assessment of dental maturity (and thus, age at death) of modern humans, extant apes, and fossil hominids. Simpson et al. (1991), Simpson (1993), Kuykendall and Conroy (1993), and Mann et al. (1987) have doubts about whether the first and third of the developmental patterns summarized above are in fact unique to apes because of questions regarding the range of variability in apes and humans and the possible developmental overlap between human and ape patterns. Issues central to this debate include 1) the range of intra- and inter-taxon variability in dental development; 2) the lack of adequate standards in interpreting hominoid dental development; and 3) questions with regard to relationships between pattern, rate, and duration of development.

Several studies have reported on variability between hominoid taxa (Conroy and Vannier, 1991a,b; Dean, 1989; Lampl and Johnston, 1993; Smith, 1991). However, of particular importance in addressing the debates cited above, is the need to document variability *within* taxa. Dental standards for humans have largely been based on well-fed

white North American children (Demirjian, 1986; Fanning, 1961; Moorrees et al., 1963). Those for great apes have been compiled from small samples of either laboratory reared animals or cross-sectional samples in which great ape genera have been lumped into a single study group (Anemone et al., 1991; Conroy and Mahoney, 1991; Dean and Wood, 1981; Kuykendall, 1992). In addition, many of the accepted standards are based solely on studies of mandibular tooth development.

Studies of non-white human populations (Fanning and Moorrees, 1969; Tompkins, 1993, 1996) have demonstrated the existence of greater variability than suggested by previous standards. In addition, studies of dental development and emergence in captive populations of chimpanzees (Anemone et al., 1993; Kuykendall and Conroy, 1993; Marzke et al., 1993) have demonstrated that there are differences between captive populations. Other studies, based on samples of known age great apes (Anemone et al., 1991; Beynon et al., 1991; Winkler et al., 1991; Winkler, in press), have also modified some of the earlier conclusions regarding the timing of great ape dental development.

Because of the need to refine the standards of ape tooth development and to better understand inherent variability, we initiated a radiographic study of orangutan dental development (Winkler et al., 1989) that built upon the work of Dean and Wood (1981). Our study differed in that it was based on a much larger sample composed primarily of wild-reared animals, included neonates, and examined all the teeth in the upper and lower dentition. The first part of this study has been published (Winkler et al., 1991) and focused on orangutan dental morphogenesis prior to alveolar emergence of any of the permanent dentition. We continue our work here by providing information on the latter phases of dental development in the orangutan, commencing with alveolar emergence of the first permanent molar through complete emergence of the permanent dentition.

## MATERIALS AND METHODS

Our cross-sectional sample included 89 orangutans: 71 were wild-reared, 9 were

TABLE 1. Distribution of *Pongo pygmaeus* specimens based on dental age

Dental age category	Number of specimens
M1 emergence <sup>1</sup>	25
M2, I1 & I2, P3 & P4, mixed emergence	24
Full permanent except for M3 and/or C	40
Total	89

<sup>1</sup>The first molars are the only permanent teeth to have completed their crowns and/or emerged into the mouth.

raised in captivity, and 9 were of unknown rearing background. Forty-four individuals were female, 32 were male, and 13 of unknown sex. All but one were of unknown age. The distribution of specimens by dental emergence category is provided in Table 1. Detailed information on the collections used, abbreviations used in the text, and radiographic techniques are provided in Table 2. As indicated in Table 2, specimens were from a variety of collections, including 40 from the Zoologische Staatssammlung, Munich (ZSM), which were captured from the same locality (Skalau). All specimens with the exception of those from ZSM were radiographed in lateral aspect by L.A.W. or J.H.S. Dr. O. Röhrer-Ertl provided us with lateral oblique and frontal radiographs of the ZSM materials. Nonscreen medical X-ray film was used for most specimens. All radiographs were developed on site to check for clarity of image. A second series of radiographs were taken of the AMNH specimens (Table 2) to improve image clarity and to better evaluate ambiguous details.

With the exception of those from CMNH (Table 2), all specimens were placed directly on the radiographic plate in order to minimize image magnification, and positioned by hand using standard landmarks for approximating the Frankfort Horizontal and aligning opposing tooth rows. The CMNH specimens were radiographed using a craniostat to align skulls in Frankfort Horizontal. With the exception of wet specimens, in which lower jaws were secured to their respective crania, mandibles were radiographed apart from the skull. Abbreviations for individual teeth follow that of Winkler et al. (1991).

The stages of tooth crown and root formation that we utilized for our analyses are

presented in Figure 1 and are in accordance with our earlier study of infant orangutans (Winkler et al., 1991; with modifications based on the work of Demirjian 1986). All teeth in both upper and lower jaws were evaluated following these criteria. Because developing crowns and roots often fell between "idealized" developmental stages, we coded intermediate stages with "+" or "-" to indicate development above or below the particular "idealized" stage. No attempt was made to estimate the state of development of missing or rotated teeth or those whose superimposed images prevented assessment of individual tooth stage. For the sake of this paper (which is based solely on radiographic analysis of tooth development), emergence was defined as alveolar emergence, or eruption above the alveolar plane (as opposed to gingival emergence).

Since the orangutan is highly sexually dimorphic, aspects of which are expressed in tooth size differences (Kay, 1982; Swindler, 1976), relative states of tooth formation were determined by comparing the radiographs of the juvenile and subadult individuals with adult specimens of the same sex. When the sex of a specimen was not known, its radiograph was compared to those of adults of both sexes so that the better match in crown shape could be assessed and thus more accurate judgements of relative tooth formation made. All radiographs, in different sequences and by different combinations of investigators, were analyzed at least 6 times in order to minimize observer error. Inter-observer variation in coding the radiographs was minimal with most differences occurring in assigning intermediate phases (+ or -) of a given developmental stage. All cases of inter-observer differences were re-evaluated by the authors until consensus was reached. Specimens were sequenced chronologically by reference to stages of M<sub>1</sub> development. Specimens similar in M<sub>1</sub> development were further discriminated by reference to M<sub>2</sub> developmental stages.

For statistical analyses and analyses of the ranges of variation, tooth development stage data from our previous study of infant orangutans (Winkler et al., 1991) were combined with those of this study (total sample = 102). Ranges of tooth development

TABLE 2. Summary of radiographic techniques

Museum <sup>1</sup>	Machine	Typical settings <sup>2</sup>	Film-source distance <sup>3</sup>	Number of specimens
ASZ	Siemens	16 mA 40 kv	100 cm	9
USNM	Keleket Dynamax Twenty	100 mA 67–68 kv 1 sec	69 cm	24
AMNH <sup>2</sup>	Hewlett-Packard Faxitron Series	3 mA 70 kv 420 sec	53 cm	7
AMNH <sup>3</sup>	Hewlett-Packard Faxitron Series	2.7 mA 72 kv 33 sec	53 cm	—
ZSM <sup>4</sup>	Siemens	50–55 kv	4–10 cm	40
CMNH	Broadbent/Bolton Roentographic Cephalometer	15 mA 70–75 kv .50 sec	152 cm	8
Pers. Coll. <sup>5</sup>	General Electric D × D 350 II	120 mA 56 Km .066 sec	102 cm	1

<sup>1</sup> Abbreviations used in Table 2 and throughout the text are USNM (National Museum of Natural History, Smithsonian Institute), AMNH (American Museum of Natural History), ASZ (Anthropologisches Institut und Museum, Universität Zurich), CMNH (Cleveland Museum of Natural History) and ZSM (Zoologische Staatssammlung, Munich).

<sup>2</sup> First series (see text for detail).

<sup>3</sup> Second series (see text for detail).

<sup>4</sup> Radiographs provided by Dr. Rohrer-Ertl.

<sup>5</sup> Specimens in personal collection of L.A. Winkler.

<sup>6</sup> Settings and distance will vary somewhat with different specimens.

stages relative to the  $M_1^I$  of a tooth's row were calculated for  $I_1^I$ ,  $C_1^I$ ,  $P_1^I$ ,  $M_2^I$ , and  $M_3^I$  (see Table 3). BMDP statistical software was then used 1) to generate bivariate regression lines, 2) to evaluate correlations (using both parametric [Pearson's  $r$ ] and nonparametric [Spearman's  $r$ ] statistics) between respective intra-individual upper and lower tooth pairs and between individual teeth in the upper and lower jaw of each specimen, and 3) to establish variability in tooth development stages relative to  $M_1^I$  of each respective jaw. For the sake of this statistical analysis, tooth stages A and B and stages I and J, respectively, were collapsed into combined stages and all stages were then converted to numeric values. Teeth which had been judged to be between developmental stages (coded with a + or – as discussed above, for example B+) were coded as .25 above or below the stage (e.g., 1.25) they approximated. In examining correlations between teeth, nonparametric statistics are more appropriate, although results from the parametric and nonparametric correlation statistics are very similar (compared in Table 4).

Although we have converted our tooth development stages to interval (numeric) data for the purpose of statistical analyses, tooth

development is not necessarily linear (Dean and Wood, 1981). For example, certain stages of tooth development may proceed more rapidly than others. Our purpose, therefore, is to examine relationships between tooth stages among teeth within individuals and not to calculate or compare rate of development between taxa or between different stages.

## RESULTS

As we reported in our earlier study of infant orangutan tooth development (Winkler et al., 1991), all permanent teeth, with the exception of  $M_3^I$ , have begun to calcify by the time the  $M_1^I$  crowns are completely formed. Seven specimens in our sample displayed one or both  $M_1^I$  in which root development had begun (stage G, Fig. 1). As demonstrated in a male wild-reared orangutan (Fig. 2a) where the first molars have not yet emerged, root development has commenced on both  $M_1^I$ , the crowns of  $M_2^I$  are approximately  $\frac{1}{2}$  developed, the incisor crowns are  $\frac{3}{4}$  developed, the crowns of the premolars are  $\frac{1}{4}$  to  $\frac{1}{2}$  developed, the crowns of the canines  $\frac{1}{4}$  to  $\frac{1}{2}$  developed.  $M_3^I$  have not yet begun to calcify. Crown development of  $M_2^I$  is relatively ad-

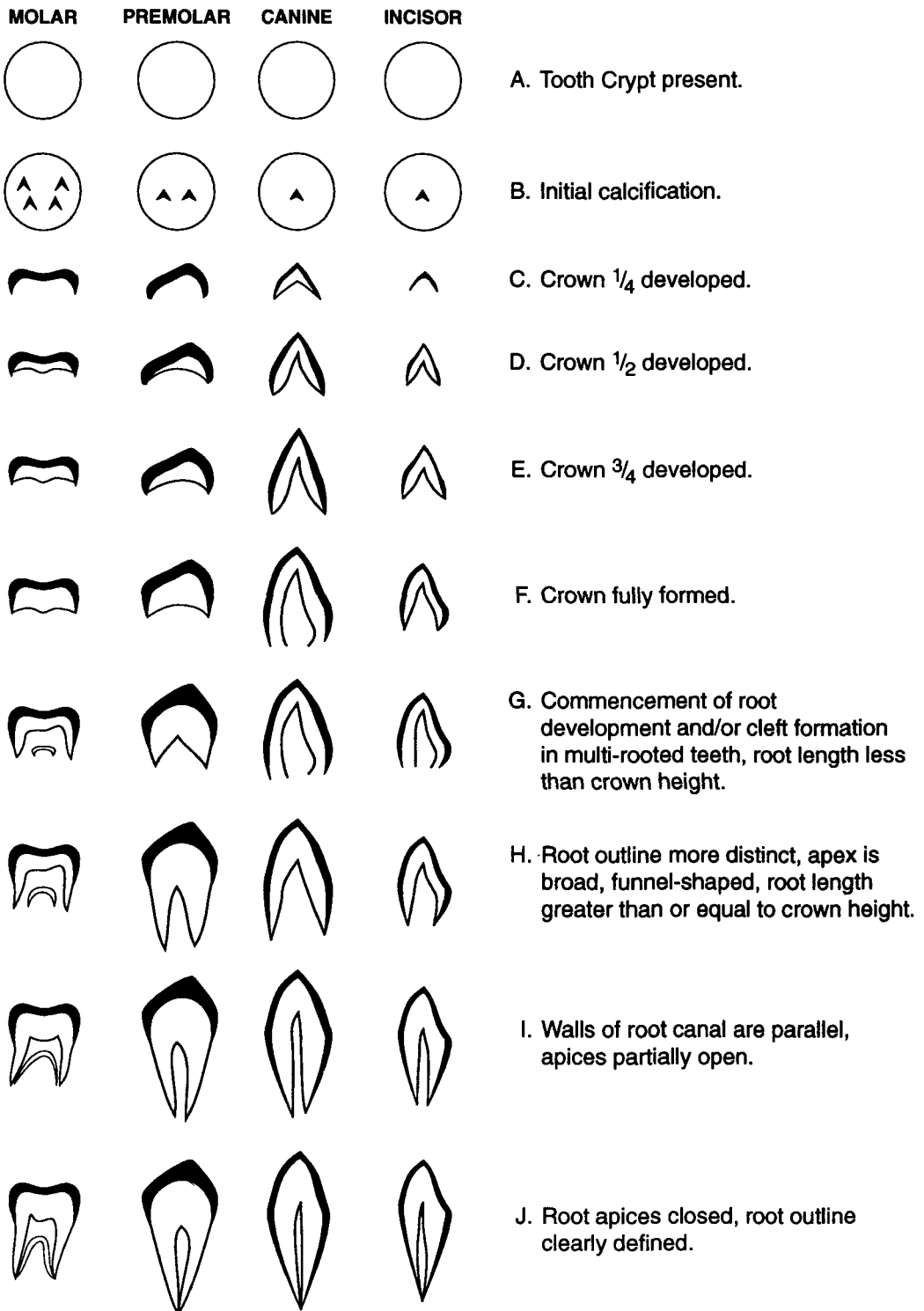


Fig. 1. Definition of tooth stages.

TABLE 3. Range of developmental stage of upper and lower permanent teeth relative to the stage of first molar development in 102 orangutans (*Pongo pygmaeus*)<sup>1</sup>

Stage of first molar	Range of stages observed				
	I1	C	P4	M2	M3
<b>Maxilla</b>					
C	C-E	B-C	C	A-B	
D	D	C	C	A-C	
E					
F	E	C	C	B-C	
G	D-F	C-D	C-D	C-E	
H	E-H	C-D	E-G	D-F	A-B
I	E-I	D-G	F-I	E-H	A-H
J	G-J	E-G	E-J	H-J	C-I
<b>Mandible</b>					
C	C	C		A	
D	D	C	C	A-C	
E					
F	E	C-D	C	C	
G	D-F	C-D	C-D	B-D	
H	D-G	C-E	D-H	C-H	A-B
I	E-I	D-G	E-I	D-H	A-H
J	H-J	E-I	G-J	G-J	F-I

<sup>1</sup>Stages as in Figure 1.

vanced in this male, whereas the stages of crown development of its other permanent teeth relative to M<sub>1</sub> lie in the middle of their respective ranges (see Table 3).

Figure 2b,c illustrates M<sub>1</sub> in the process of alveolar emergence and M<sub>1</sub> nearly in full occlusion. Although a crypt for M<sub>3</sub> is visible in this male wild-reared specimen, the remaining permanent teeth as well as M<sub>1</sub> are relatively similar to those in Figure 2a. Note that very little root has developed on M<sub>1</sub> compared to the M<sub>1</sub>. Crypts for M<sub>3</sub> are visible in both the upper and lower jaws of another specimen (Fig. 2d), which possesses M<sub>1</sub> in full occlusion with fairly advanced root development, M<sub>2</sub> with crowns  $\frac{3}{4}$  complete, premolars and incisors with nearly complete crowns, and canines with crowns which are  $\frac{1}{4}$  to  $\frac{1}{2}$  developed.

There is variability in which permanent tooth emerges after M<sub>1</sub>. As seen in Figure 3a-d, the incisors, particularly I<sub>1</sub>, generally precede M<sub>2</sub> in emergence. However, in our sample, the second molars had emerged prior to I<sub>1</sub> in 5 cases. I<sub>1</sub> and M<sub>2</sub> are emerging in tandem in several others. I<sub>2</sub> appear to

closely follow the central incisor in emergence. At the time of their emergence, the incisors possess more root (generally in stage H) than do the emerging M<sub>1</sub>. The second molars also possess more root at emergence than do the first molars, but the difference is not as substantial as between the incisors and the first molars.

In the four specimens in Figure 3, M<sub>1</sub> are in occlusion and root development has commenced on M<sub>2</sub>. Except for some variation in the amount of root development on the premolars, and in differences in the degree of crown development of the canines (compare the two females in Figure 3a and 3d and the male in Fig. 3c), the stages of tooth development are remarkably similar. Most of the variability is in the emergence status of the permanent teeth. Thus, in one specimen (Fig. 3a), only M<sub>1</sub> is fully emerged, although M<sub>2</sub> is near alveolar emergence. In a second specimen with unemerged M<sub>2</sub> (Fig. 3b), the deciduous incisors are being displaced and the permanent incisors are emerging. One of the upper central incisors has emerged in a third juvenile orangutan in Figure 3c with unemerged M<sub>2</sub>. All the permanent incisors have emerged or are in the process in a fourth orangutan (Fig. 3d).

The premolars appear to emerge after the incisors and M<sub>2</sub>. When they emerge, the premolars possess a greater amount of root development than do either M<sub>1</sub> or M<sub>2</sub>. In our sample, the canines generally follow the premolars in emergence, with M<sub>3</sub> emerging into occlusion last. (However, in two specimens, the canines remain unemerged while the remainder of the permanent dentition is in occlusion [see Fig. 4]). M<sub>3</sub> have more root present at emergence than either M<sub>1</sub>-<sub>2</sub>, but the difference in amount of root formation is relative and variable. The canine, particularly C<sub>1</sub>, has more root at emergence than does any other tooth in the jaw (see Fig. 4).

As mentioned above, Table 3 presents the ranges of tooth development of I<sub>1</sub>, C<sub>1</sub>, P<sub>4</sub>, M<sub>2</sub>, and M<sub>3</sub> relative to each stage of M<sub>1</sub>. The

TABLE 4. Bivariate analysis of development of upper and lower tooth pairs

Correlation coefficient	I <sub>1</sub> -I <sub>1</sub>	I <sub>2</sub> -I <sub>2</sub>	C <sub>1</sub> -C <sub>1</sub>	P <sub>3</sub> -P <sub>3</sub>	P <sub>4</sub> -P <sub>4</sub>	M <sub>1</sub> -M <sub>1</sub>	M <sub>2</sub> -M <sub>2</sub>	M <sub>3</sub> -M <sub>3</sub>
Pearson's r	.964	.958	.969	.961	.971	.982	.980	.960
Spearman's r	.938	.953	.966	.957	.962	.952	.957	.960

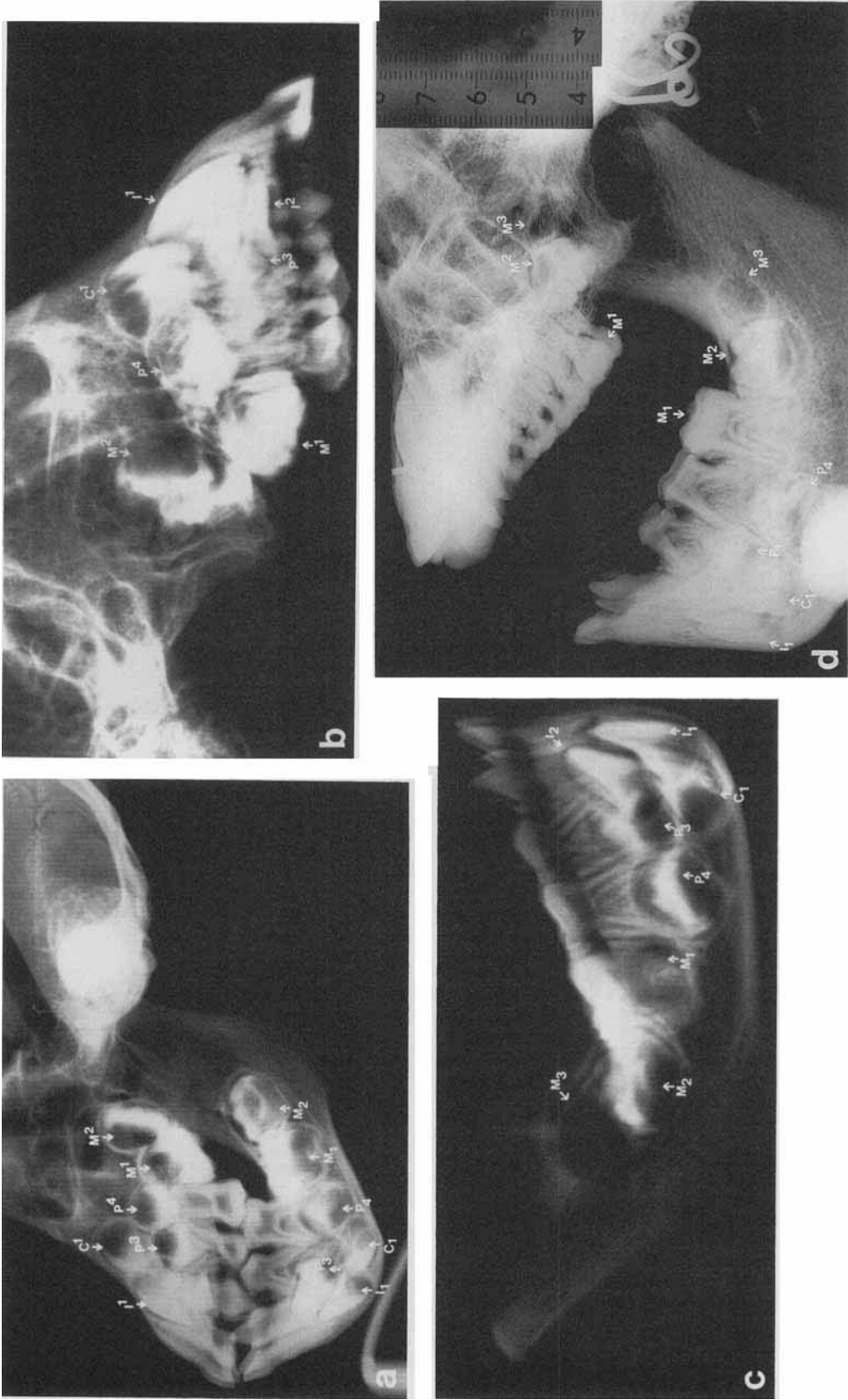


Fig. 2. **a:** The developing dentition of a male wild-captured orangutan (CMNB B164) with root development commencing on  $M_1^l$  (which has not yet emerged). Not to scale. **b,c:** The upper (b) and lower (c) jaws of a male wild-reared orangutan (AZ 1566) with  $M_1^l$  emerging into occlusion. Not to scale. **d:** The crypts of  $M_3^l$  can be identified in this orangutan (AMNH 90395) where the crowns of  $M_2^l$  are not yet complete. Note that  $M_1^l$  are the only permanent teeth in occlusion. Not to scale.

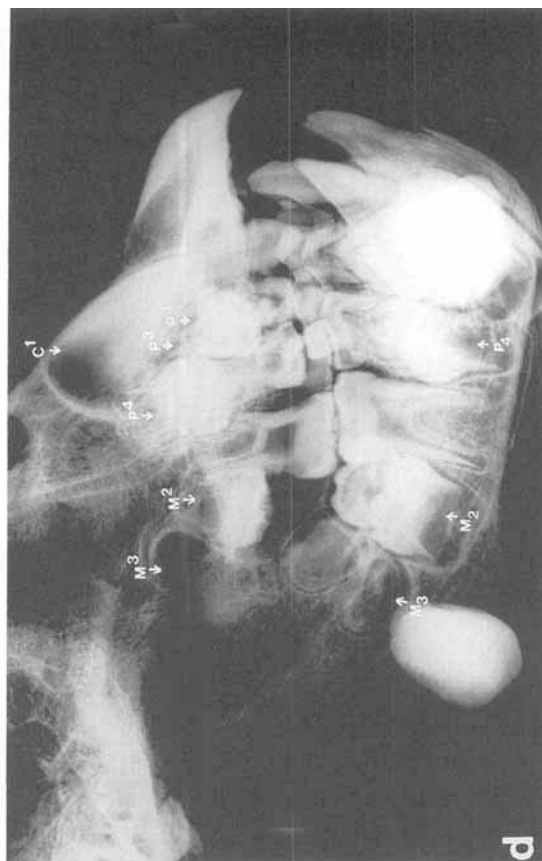
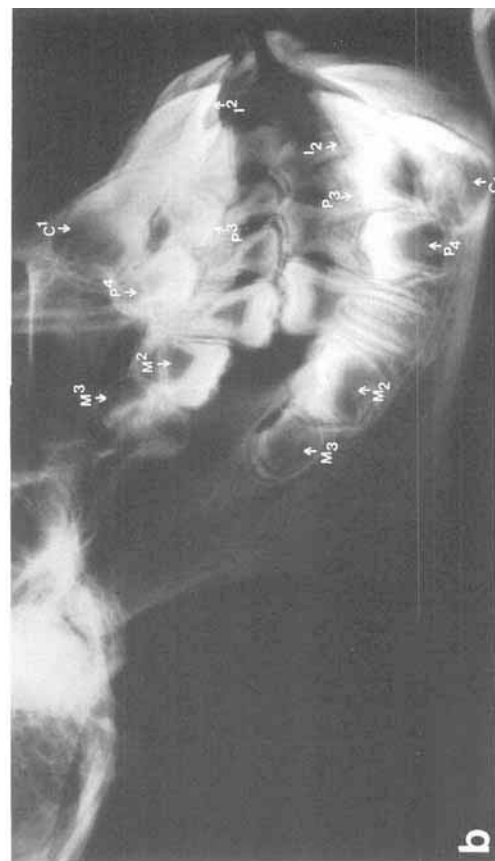
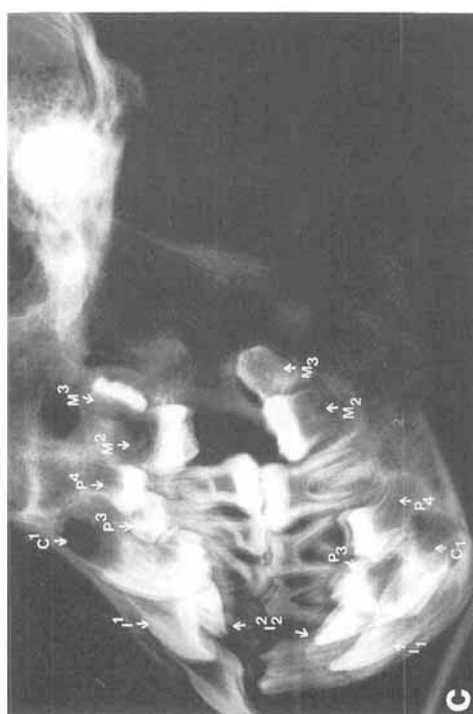


Fig. 3. **a:**  $M^2$  is near alveolar emergence in this female wild-reared orangutan (ZSM 115). Note the lack of incisor alveolar emergence. Not to scale. **b:** The permanent incisors are beginning to displace the deciduous incisors in this female wild-reared orangutan (CMNH 1024) with  $M^2$  near alveolar emergence. Not to scale. **c:** Root development has begun on  $M_2$  and one  $I^1$  has emerged into occlusion in this wild-reared orangutan (CMNH 1397) with  $M_3^1$  which have not yet emerged. Not to scale. **d:** The incisors are either fully or partially emerged in this male zoo-reared orangutan (AMNH 35164) with unerupted  $M_2^1$ . Note that the crowns of  $M_3^1$  in this animal are less developed than that seen in Figure 3a. Not to scale.



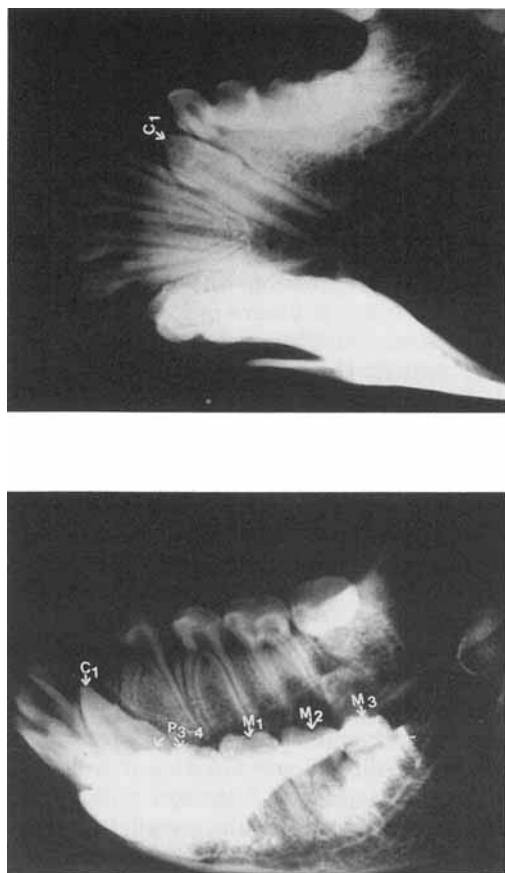


Fig. 4. The permanent dentition is nearly complete in this lateral oblique radiograph (taken from behind the mandible [above] and lateral to the mandible with the jaw rotated obliquely [below]) wild-reared male (ZSM 79), where  $C_1$  is in the process of emergence. Note the extensive root formation on  $C_1$ .  $M_3$  has erupted on both sides of the jaw but lost on one side postmortem. Not to scale.

sample for the stages of crown development of  $M_1$  (stages C–F) is limited to 12 specimens, which restricts the variability seen. However, even with this limited sample, during  $M_1$  crown development several teeth ( $I^1$ ,  $C^1$ ,  $M_2^1$ ) demonstrate a two- to three-stage range compared to the same teeth in other specimens with  $M_1$  at the same stage of development. At first glance, there might appear to be much more variation in the development of the other permanent teeth during the latter stages of first molar development (G–J). However, it takes  $M_1$  relatively longer peri-

ods of time to develop their roots than their crown; thus the greater range of tooth development stages for the other teeth during  $M_1$  root development is a reflection of the longer period of time that root development encompasses (Dean et al., 1993a; Moorrees et al., 1963), not of greater variability.

Table 3 provides data pertinent to issues raised in the introduction regarding range of variability as well as the discrimination of ape and human developmental patterns. Stage of incisor crown development in some cases appears to parallel stage of first molar crown development (see Table 3). However, in all relevant specimens, the first molar crowns are complete prior to completion of  $I^1$ . Furthermore, as discussed above, the first molars emerge with very little root development (stage G or early H). In the several specimens with some stage of  $M_1$  emergence, none of the central incisors had any root formation although the incisor crowns were fully formed in some specimens.

Table 3 clearly demonstrates developmental overlap between the crowns of  $M_1^1$  and  $M_2^1$ . In some cases, crypts for  $M_2^1$  are present when first molar crowns are only  $\frac{1}{2}$  developed. In other cases, the crowns of  $M_2^1$  are just beginning to calcify at the time when the  $M_1^1$  are complete or commencing root development.

Tables 4–7 and Figures 5 and 6 present the results of the statistical analyses. Previous authors (Dean and Wood, 1981; Simpson et al., 1991) have reported few qualitative differences in the development of upper and lower tooth pairs in apes or humans (isomeres, per Garn and Smith, 1980). The high correlation coefficients and slopes seen in Table 4 between isomeres suggest isochrony, clearly supporting these earlier findings.

Tables 4 and 5 indicate high correlations between most of the comparisons of tooth pairs within the jaw of each individual. The highest correlations exist between the central and lateral incisors, the incisors and the premolars, the incisors and  $M_2^1$ , and the premolars and  $M_2^1$ . The premolars and  $M_2^1$  commence calcification at approximately the same time (Beynon et al., 1991; Winkler et al., 1991) and these particular clusters of teeth emerge in rapid succession, which partially explains the high correlations. Al-

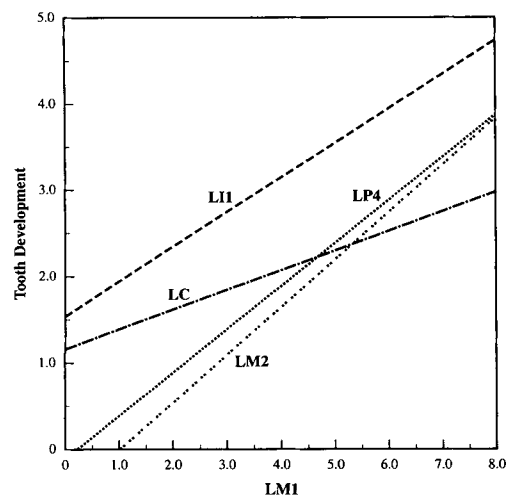


Fig. 5. Lower tooth development relative to M1.

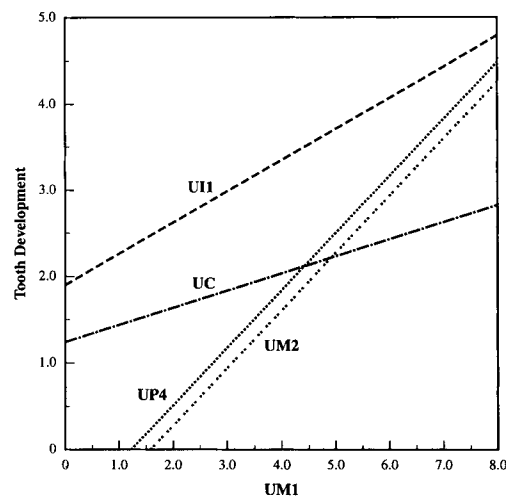


Fig. 6. Upper tooth development relative to M1.

though the third molars and canines also emerge in rapid succession, the correlations for these teeth are lower than the previously mentioned tooth pairs, which is undoubtedly due to the earlier onset of calcification and longer developmental period of the canines relative to that of  $M_3^3$  (Beynon et al., 1991; Dean et al., 1993a; Winkler et al., 1991; Winkler, in press).

Bivariate regression lines for  $I_1^1$ ,  $C_1^1$ ,  $P_4^4$ , and  $M_2^2$  relative to stages of  $M_1^1$  development are presented in Figures 5 and 6. Slopes and intercepts for these lines are provided in Table 7. The graphs reinforce Tables 5 and 6 in indicating close parallels between the developmental stages of  $P_4^4$  and  $M_2^2$ . The graphed regression lines also clearly demonstrate the comparatively longer developmental period of  $C_1^1$ .

DISCUSSION

Our large sample and the ability to study all teeth in the dentition have allowed us to better examine variability in great ape dental development and to clarify recent debates regarding characteristics of great ape dental development. Although differing in details, our overall results parallel in many ways those of Dean and Wood's earlier study (1981) of dental development in the great apes. However, our results demonstrate a relatively large range of variability in individual tooth development and in patterns of development. Since the ranges of certain aspects of proposed great ape and human patterns may overlap because of this variability (Fanning and Moorrees, 1969; Simpson, 1993), precise differentiation between great ape and human dental patterns may be difficult. The results of this study on the orangutan provide additional evidence to

TABLE 5. Correlation coefficients (Spearman's *r*) for bivariate comparisons of the lower dentition in a sample of 102 orangutans (*Pongo pygmaeus*)

	$I_1$	$I_2$	$C_1$	$P_3$	$P_4$	$M_1$	$M_2$	$M_3$
$I_1$		.971	.912	.935	.924	.837	.910	.875
$I_2$	.971		.915	.935	.924	.807	.915	.896
$C_1$	.912	.915		.898	.891	.776	.884	.843
$P_3$	.935	.935	.898		.989	.803	.945	.924
$P_4$	.924	.924	.891	.989		.753	.961	.918
$M_1$	.837	.807	.776	.803	.754		.779	.460
$M_2$	.910	.915	.884	.945	.941	.779		.888
$M_3$	.875	.896	.843	.924	.918	.460	.888	

TABLE 6. Correlation coefficients (Spearman's  $r$ ) for bivariate comparisons of upper dentition in a sample of 102 orangutans (*Pongo pygmaeus*)

	I <sup>1</sup>	I <sup>2</sup>	C <sup>1</sup>	P <sup>3</sup>	P <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>
I <sup>1</sup>		.970	.904	.928	.934	.838	.934	.857
I <sup>2</sup>	.970		.891	.942	.960	.824	.934	.846
C <sup>1</sup>	.904	.891		.891	.891	.783	.878	.847
P <sup>3</sup>	.928	.942	.891		.978	.823	.936	.854
P <sup>4</sup>	.934	.960	.891	.978		.805	.948	.877
M <sup>1</sup>	.838	.824	.783	.823	.805		.824	.402
M <sup>2</sup>	.934	.934	.878	.936	.948	.824		.845
M <sup>3</sup>	.857	.846	.847	.854	.877	.402	.845	

TABLE 7. Bivariate regression equations for lower and upper teeth relative to M<sup>1</sup> in a sample of 102 orangutans (*Pongo pygmaeus*)<sup>1</sup>

	Equation	R
I <sub>1</sub> -M <sub>1</sub>	Y = -1.6563 + 1.1001x	.802
C <sub>1</sub> -M <sub>1</sub>	Y = -1.5914 + .85779x	.651
P <sub>4</sub> -M <sub>1</sub>	Y = -6.2101 + 1.6191x	.782
M <sub>2</sub> -M <sub>1</sub>	Y = -4.0646 + 1.3225x	.802
M <sub>3</sub> -M <sub>1</sub>	Y = -18.547 + 2.8363x	.442
I <sup>1</sup> -M <sup>1</sup>	Y = -.57528 + .94163x	.798
C <sup>1</sup> -M <sup>1</sup>	Y = -1.5189 + .83385x	.623
P <sup>4</sup> -M <sup>1</sup>	Y = -5.5636 + 1.5476x	.815
M <sup>2</sup> -M <sup>1</sup>	Y = 5.9152 + 1.5930x	.837
M <sup>3</sup> -M <sup>1</sup>	Y = 21.406 + 3.2103x	.429

<sup>1</sup> Equations graphed in Figures 5 and 6.

evaluate the degree of variability and, hence, proposed differences between great apes and humans (as discussed in the introduction) as well as other issues.

### I<sub>1</sub>/M<sub>1</sub> relationships

Our results clearly reaffirm that there are differences between humans and great apes in the timing of crown development and emergence of M<sub>1</sub> relative to the stages of dental development of I<sub>1</sub>. Earlier studies in great apes (Beynon et al., 1991; Dean and Wood, 1981; Winkler et al., 1991) indicate that I<sub>1</sub> begin calcification several months after M<sub>1</sub>. A similar pattern of calcification commencement between the teeth exists in humans (Smith, 1991). However, in humans, despite differences in calcification commencement, these teeth emerge at approximately the same time. But, in the orangutan, there is a one- to two-stage delay in crown development of I<sub>1</sub> relative to M<sub>1</sub> at all stages of development prior to, and at M<sub>1</sub> emergence (see Winkler et al., 1991, for discussion of neonatal development). Our findings are thus in agreement with similar results obtained in studies of this relationship in Afri-

can apes (Anemone et al., 1996; Dean and Wood, 1981; Simpson et al., 1991). However, whereas Anemone et al. (1996) report that the lower incisor crowns are incomplete at M<sub>1</sub> emergence in the chimpanzee, this condition is variable in the orangutan with the crowns of I<sub>1</sub> being incomplete in some cases and complete in others where M<sub>1</sub> emergence is occurring or where M<sub>1</sub> has completed emergence into occlusion. (see Table 3).

Differences between great apes and humans in M<sub>1</sub>/I<sub>1</sub> developmental patterns (particularly in the degree of root development on I<sub>1</sub> at M<sub>1</sub> emergence) are of the same sort as those reported between the gracile and robust australopithecines (Conroy, 1988; Conroy and Vannier, 1991a,b; Dean and Wood, 1981; Dean, 1985; Grine, 1987; Smith, 1986). The robust forms frequently show some degree of root development on I<sub>1</sub> at M<sub>1</sub> emergence similar to the I<sub>1</sub>/M<sub>1</sub> pattern reported for some human populations (Dean, 1985; Moorrees et al., 1963; Smith, 1991). In contrast, similar to the pattern seen in our orangutan sample and reported elsewhere for great apes (Dean and Wood, 1981), the gracile forms do not possess root development on I<sub>1</sub> at M<sub>1</sub> emergence. It is noteworthy that this difference between the gracile and robust australopithecines are beyond the range of variability seen in our sample.

The amount of root development on orangutan incisors after M<sub>1</sub> emergence, but prior to their own emergence and the emergence of M<sub>2</sub>, varies widely. In general, relative root length and size varies substantially between orangutans of the same emergence status. Variability in root developmental length seen here is similar to that reported by Conroy and Vannier (1991a) in their comparisons of two immature gracile australopithe-

cines (Taung child, STS 151–161) (compare incisor root development between Fig. 2d and Fig. 3a–c).

### Sequential molar overlap

The timing of molar calcification commencement of the second and third molar relative to the crown development stage of the first and second molar, respectively, showed interesting variation in our orangutan sample. For instance, a crypt or other evidence of calcification commencement may occur in a second or third molar prior to attainment of crown completion stage in the previous sequential molar in that tooth row. In other cases where a first or second molar tooth is at the stage of crown completion, the sequential molar behind it in the tooth row is at initial calcification stages (Fig. 1, stages A or B).

Previous studies of great ape molar development (Anemone et al., 1991, 1993) that suggested a greater degree of developmental overlap between molar crowns with  $M_2^1$  commencing calcification prior to crown completion of  $M_1^1$  are within the range of variability seen in this study. Such overlap is illustrated in Figure 6b of our earlier paper on orangutan dental formation during infancy (Winkler et al., 1991), where a crypt for  $M_2$  is visible posterior to the developing crown of  $M_1$ . However, in agreement with Kuykendall and Conroy (1993), we found the variability too high to consistently predict crown calcification stage overlap with a sequential molar always commencing calcification *prior* to crown completion of a previous molar. However, as a general rule, a sequential molar had always begun calcification by the time a previous molar crown reached completion and began root development (as predicted by Dean and Wood, 1981). This pattern appears to be true for both chimpanzees and orangutans.

Previous authors (Dean et al., 1993b; Fanning and Moorrees, 1969; Simpson, 1993) have suggested that the pattern of molar crown calcification overlap may not be unique to great apes but may also occur variably in humans. If, as suggested, it is a variation common to some human populations, then it may not be useful in distinguishing humans from great apes. Simpson (1993)

and Conroy and Mahoney (1991) have provided evidence of some degree of overlap in sequential developing molar patterns between chimpanzees and humans. In addition, some degree of sequential molar crown calcification overlap also occurs in some Old World monkeys (Sirianni and Swindler, 1985), with overlapping ranges between crown completion of  $M_1^1$  and initial calcification of  $M_2^1$  and between crown completion of  $M_2^1$  and initial calcification of  $M_3^1$  in *Macaca nemestrina*.

### Canine development

Our results corroborate previous reports (Dean and Wood, 1981) of a much longer development of  $C_1^1$  in the apes compared to modern humans. Our earlier studies and those of others (Beynon et al., 1991; Dean et al., 1993a; Winkler, in press) indicate that, in the orangutan, the canine commences calcification shortly after birth. In fact, a permanent canine was found to be commencing calcification at birth in one newborn male (Winkler, in press). In the maxilla, it appears to be the second or third permanent tooth to begin calcification after  $M^1$ . However, as discussed above, it is among the last tooth to emerge in both jaws.

The time period reported for canine commencement in the orangutan (Beynon et al., 1991; Dean et al., 1993a; Winkler, in press) differs in being earlier than that reported for the chimpanzee (Anemone et al., 1991; Dean and Wood, 1981). This may be an actual difference between these great apes or it may reflect the different methodologies used in establishing crown commencement. Evidence for the orangutan is based on histological studies of crown development (Beynon et al., 1991) and on calcified teeth found upon dissection. Crown calcification data for the chimpanzee are based solely on studies of radiographs (Anemone et al., 1991; Dean and Wood, 1981) which can underestimate crown calcification status (Dean and Wood, 1981; Hess et al., 1932; Winkler, in press). In fact, a recent study by one of the authors (Winkler, in press) comparing radiographic evidence of tooth development in infant apes with the dissected evidence of tooth development in the same animals found that underestimation of tooth development from radio-

graphs is particularly problematic in early stages of calcification.

### Variation in emergence sequence

In our study of the orangutan, we have found several variants from the common emergence pattern of  $M_1-I_1-I_2-M_2-[P_3-P_4]-C_1-M_3$  previously reported for great apes (Swindler, 1985). Although  $I_1$  and  $I_2$  often follow  $M_1$  in the emergence sequence in the orangutan (as discussed in our Results), our data indicate that  $M_2$  emergence may precede one or both of these teeth in some specimens. This observation is similar to earlier reports of these pattern or sequence variants in the orangutan (Brandes, 1928, 1931, 1939; Schultz, 1935, 1941; Selenka, 1998) and in the chimpanzee (Conroy and Mahoney, 1991; Schultz, 1940).

Our sample also demonstrates  $C_1-M_3$  emergence sequence variability. One or both canines generally precede the third molars in emergence. However, in two males, the emergence of the third molars precedes that of the canines.  $C_1-M_3$  emergence sequence variability has been reported by others (Krogman, 1930; Schultz, 1941) and appears to be most likely to occur in males.

Despite reports of  $M_2-P_4/P_4-M_2$  sequence variants in chimpanzees, gorillas, fossil hominids, and in humans (Conroy and Vannier, 1991a; Garn and Burdi, 1971; Garn et al., 1956; Swindler, 1985; Willoughby, 1978), we found no evidence of these sequence variants in the orangutan. Although we were not able to delineate  $P_3-P_4$  emergence sequences in our sample, all these teeth emerged after  $M_2$  in all pertinent specimens in our sample, despite the fact that the  $P_4$  and  $M_2$  tended to be at similar stages of development prior to emergence (see Figs. 5 and 6 and discussion regarding Tables 5 and 6).

### Root development

In concordance with earlier studies of great ape dentition (Dean and Wood, 1981; Swindler, 1985), we also found differences in the amount of root development on each of the sequential molars at the time of emergence, with  $M_1$  having relatively little root ( $\frac{1}{4}$  or less) at emergence, more root on  $M_2$  at emergence relative to  $M_1$ , and slightly more on  $M_3$  at emergence relative to  $M_2$ . However,

although the amount of root at emergence tends to increase with sequential molars, we found the increased amount of root to be highly variable and most of the molar teeth that we observed emerging had less than half of total root formation complete. Nevertheless, our results substantiate reports of relatively limited root development on the great ape  $M_1$  at their emergence in contrast to the human  $M_1$  which has relatively more root at emergence (Dean and Wood, 1981; Swindler, 1985).

### CONCLUSIONS

As discussed above, our results establish a relatively large range of variability in individual tooth development and in patterns of development, including emergence sequence patterns. Several teeth demonstrate a 2–3-stage range in development relative to a specific stage of  $M_1$ . This study also demonstrates variability in the degree of temporal overlap between sequential molar crown development. In addition, although we found that the amount of root at emergence tends to increase with sequential molars, the increased amount of root is highly variable.

Our results reaffirm earlier reports (Dean and Wood, 1981) of differences between humans and ape patterns of  $I_1/M_1$  and  $C_1$  development. In addition, the timing and patterns of development of these teeth in the orangutan differ in some ways from published reports (Anemone et al., 1991, 1996; Dean and Wood, 1981) of chimpanzee development.

Results of our statistical analyses indicate high correlations between maxillary and mandibular tooth pairs. High correlations were also found between many of the teeth within the jaws of individuals with the highest correlations between teeth that commence calcification at nearly the same time and then subsequently erupt together.

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